On the Affinities of the Genus *Madrepora*.

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The Linnean genus *Madrepora* was restricted approximately to its present limits by Lamarck, although as now understood it includes certain species which were referred by him to the genera *Oculina* and *Astræa*. Although few genera of corals appear so well defined and so readily recognized, its relation to other genera of the Perforata is a question on which there has been much diversity of opinion. Dana, in 1848, instituted a family Madreporidæ for the reception of the genera *Madrepora* and *Manopora* (=*Montipora*, Oken, which has priority). Klunzinger (1879) and Ridley (1884) have since adopted this arrangement. On the other hand, Milne-Edwards and Haime (1860) separated the two genera by a considerable interval in the classification which they proposed. According to these authors the family Madreporidæ should have a much wider range and include three subfamilies, viz. :—Eupsammin æ, Madreporinæ (confined to the genus *Madrepora*), and Turbinariinæ. They proposed that the genus *Montipora* should form a subfamily (Montiporinæ) of the Poritidæ. Verrill in 1865 also included *Montipora* with the Poritidæ and placed *Madrepora* and *Turbinaria* in separate families. In 1868, however, he followed Dana in associating *Madrepora* and *Montipora* together in one family. Duncan, in his Revision of the Madreporaria, read before this Society in 1885, followed Edwards and Haime in the association of *Montipora* with the Poritidæ, but extended the family Madreporidæ so as to include *Turbinaria*, *Astræopora*, and their fossil allies. Quelch has proposed still different limits for the family Madreporidæ, which he regards as including the following recent genera:—*Madrepora*, *Turbinaria*, *Astræopora*, *Anacropora*, *Montipora*. Finally Ortmann has recently (1890) proposed a new classification of the Madreporaria in which the genera *Madrepora* and *Montipora* rank as families ; the former is placed between the Alveoporidæ and the Eupsammidæ, the latter between the Turbinariidæ and the Poritidæ.

A discussion of the affinities of the genus *Madrepora* may appropriately commence with a criticism of the views of Duncan

as to the interrelationships of the genera *Madrepora*, *Turbinaria*, *Montipora*, and *Porites*. The only essential distinction between the families Madreporidæ and Poritidæ, according to the diagnoses given by Duncan, is to be found in the condition of the septa; in the Madreporidæ these are stated to be lamellar, slightly porous, or solid; in the Poritidæ never completely lamellar and often trabecular. This distinction may be satisfactory so far as *Turbinaria* and *Porites* are concerned, but would probably not have been regarded by Duncan as the most important difference between the two genera. In my experience the distinction does not hold good for all species of *Madrepora* and *Montipora*. In *Madrepora* one frequently meets with specimens in which the septa are not lamellar, especially in species in which they are never well-developed, and on the other hand many species of *Montipora* have well-developed lamellar septa. Duncan noted in an earlier paper, which will shortly be referred to, that in the genus *Madrepora* the septa are first recognizable (in bud-corallites) as longitudinal series of spinose trabeculæ projecting inwards from the thin porous wall; and I find that in some species the lower part of the septa never passes beyond this stage. The condition of the septa thus furnishes evidence for the union of *Madrepora* and *Montipora* into one family rather than for their separation. On looking elsewhere for the family characters, one cannot fail to notice the close general resemblance between *Madrepora*, *Anacropora*, and *Montipora*, and their equally distinct separation from *Turbinaria* and its allies on the one hand and *Porites* and its allies on the other. Indeed the separation into three groups is so marked that, excepting in the trabeculate origin of the septa, one fails to find any close relationship between the genera *Montipora* and *Anacropora* and the remaining Poritinæ *in sensu* Duncan.

Duncan in 1884 gave an account of the structure of the corallum in certain species of *Madrepora*. He pointed out that in young corallites the wall has only one layer of mural tissue, which is costulate, finely serrate or echinulate exteriorly, according to the species. An increase in mural tissue takes place by the formation of a new layer around the costulate or echinulate surface, in such a way that the costulæ or spinules act as props for the newly-formed layer, and the space between adjoining props is converted into a more or less completely closed chamber.

In transverse section "concentric circles of thin calcareous structure are seen, separated by radiating linear pillars; the circles having been in turn outside wall and the radii either spinules or costæ." If the coral is old the inner circles of tissue next the septal cavity are dense. Duncan also pointed out that no communication exists between the cavities of bud and axial corallites "except in a very indirect manner and through the medium of the dermal structures. . . . . Budding takes place remote from the calicular margin and may arise from sclerenchyma remote from the wall of a corallite." Thus the density of the corallite depends to a great extent on the breadth of the so-called costæ and is always densest where the costæ are replaced by fine echinulations.

A further point remains to be noticed which appears to me important. As a result of the peculiar mode of budding in the genus *Madrepora*—which leads to the formation of a type of colony termed "patrioramose" by Dana—there is no cœnenchyma in the true sense of the word excepting at points where the colony is incrusting. The radial corallites are arranged on the branches at variable intervals, and the space between them is usually considered to consist of cœnenchyma; but these intervals really form part of the thickened wall of the axial corallite around which the radial corallites are developed, and the trabecular network of which they are composed is not precisely comparable with the interzooidal cœnenchyma of *Turbinaria*, for example, which is a true secretion of interzooidal tissue and not of the walls of the zooids themselves.

The skeletal structure of the genera *Anacropora*, *Montipora*, *Porites*, and *Turbinaria* has hitherto received little attention. I have not as yet made a complete study of the question; the following notes are based on the study of only one or two species in each genus and, though sufficient for my present purpose, may need revision later. In *Anacropora* and branching species of *Montipora* the axis of a branch is occupied by elongate fibrous trabeculæ similar to those which constitute the trabecular type of columella in most genera of Madreporaria. Around this axial mass a network of shorter processes occurs in which the corallites are embedded; the intervals between the corallites consist of true cœnenchyma. The mode of budding is intercalicular but apparently the individual corallites remain directly connected together; in any case the stolon-like canals by which they are

united is not so intricate as in *Madrepora*. In lobose species of *Porites* the centre of each lobe consists of an open network of tissue, and the peripheral parts in which the corallites are imbedded has a similar structure, but the corallites are shallow and differ considerably in structure from those of *Montipora*. In *Porites* and its allies the budding may be inter- or intra-calicular and the corallites remain in direct communication with one another. Owing to the fact that the walls of adjoining corallites become fused together, there is little or no cœnenchyma between them. In the case of *Turbinaria* budding takes place by means of serial, radially-directed stolons, each more distal corallite being directly connected with the base of the one behind it. The radiating series of corallites are connected together by true cœnenchyma.

It will next be necessary to give a short summary of the structure of the soft tissues so far as this is known at present. Fowler has studied two 'Challenger' species, in one of which an interesting and new type of dimorphism occurs. The following short summary of his results gives the chief points of interest for my present purpose.

1. The external body-wall consists of ectoderm, mesoglœa, and entoderm. Under this and between the costæ a series of external longitudinal canals exists, which open into each other and also through the corallum into a series of internal canals with radial and transverse connections; these in turn communicate with the general cœlentera of the polyps, and all communicate eventually with the cœlenteron of the axial polyp.

2. The structure of the polyps is in its general features Actinian, but there is a marked bilateral arrangement of the parts. The septa are probably entocœlic. There are twelve mesenteries; six are short, the others longer, but two of these are very long and are the only ones which bear reproductive organs. Similar elongate mesenteries occur in Alcyonaria, in Antipatharia, and in *Seriatopora* and *Pocillifera* amongst the Madreporaria. In Antipatharia, as in *Madrepora*, they are the only ones which bear reproductive organs.

Since the publication of Fowler's observations, our views as to the homologies of the mesenteries of Zoantharia have undergone considerable modification, due more especially to the researches of Haddon and McMurrich on Actiniaria and my own on Antipatharia. Fowler's division of the peripheral portions of the

polyp-cavity into endocœles and exocœles is only applicable to forms in which the mesenteries are arranged on the Hexactinian plan, *i. e.* in so-called pairs consisting of adjacent mesenteries. The development of mesenteries in such pairs only commences after the first twelve are formed. Up to that point the arrangement is bilateral and members of a pair are situated on opposite sides of the stomodæum; the only ones which come to form pairs in the Hexactinian sense are the directives. It therefore now appears necessary to make use of another term to distinguish the inter-mesenterial chambers in bilateral types with 6, 8, 10, 12, or more mesenteries, and the word "amphicœle" appears suitable. I would use the term in all cases of Anthozoa where the lateral divisions of the cœlenteron are brought about by the formation of mesenteries arising from opposite sides of the stomodæum and where in consequence the chambers are simply intermesenterial; in other words, in homocœlic as distinguished from heterocœlic types. In such cases the position of the retractor muscles of the mesenteries is variable and may or may not correspond with the Hexactinian arrangement. In the case of *Madrepora* the arrangement is Hexactinian, that is to say the mesenteries are arranged in real or apparent pairs, having the retractor muscles on their outer surfaces in the case of the directives and on the inner surfaces in all other cases. Using Fowler's terminology the primary septa (6) are, in *Madrepora*, endocœlic, the secondary cycle (6) exocœlic. Although the development of *Madrepora* is not known, I think one is justified from our knowledge of the development of Hexactinians, and Haddon's observations on the embryo of *Euphyllia*, in concluding that in the final arrangement only the directive mesenteries arose as pairs and that the other pairs consist of mesenteries situated on opposite sides of the stomodæum. In this case the arrangement of the retractor muscles does not indicate the true relationship of the lateral mesenteries and all the septa should be described as amphicœlic.

I would also suggest that the septa situated between the "directive" mesenteries be known as the "directive" septa, as they indicate the long axis of the stomodæum and are the first to indicate a bilateral arrangement of parts in the skeleton. It is often stated as characteristic of the genus *Madrepora* that the directive septa are more prominent than the other primaries; but this is by no means always the case, nor is the feature con-

fined to the genus. One frequently finds that in radial corallites the outer directive septum is broad and the other five primaries equal. In other species the primary septa of both axial and radial corallites are of equal breadth, in which case the bilateral arrangement of parts in the polyp is not indicated by the relative importance of the directive septa. Unfortunately we yet know little of the structure of the polyps in the genera *Anacropora* and *Montipora*, but the relative importance of their septa is subject to the same variations as in *Madrepora*. In *Anacropora* the corallites are prominent, and the branches resemble those of *Madrepora* so closely that it is not until the absence of an axial corallite is observed that the generic distinction is realized. In this genus the directive septa are usually broader than the others. In *Montipora* the septa are sometimes all rudimentary, but in other cases the directives are very broad and may even meet in the middle line to form a false columella such as occurs in certain species of *Madrepora*. A bilateral arrangement of parts is thus as well marked by the septa of *Anacropora* and *Montipora* as in *Madrepora*, and one may infer a somewhat similar structure in the polyps. The polyps of *Porites* have not been studied, but they bear no external resemblance to those of *Madrepora*. Fowler also has shown that the polyps of *Turbinaria* do not conform to the *Madrepora* type.

Ridley, in 1884, discussed the mode of budding in *Madrepora* and *Montipora*, and considered that there is a fundamental difference between the two types, dependent on the terminality or non-terminality of the distal corallite. He pointed out that *Isopora*, Studer (a subgenus of *Madrepora*), is not without apical corallites as had been supposed, but that each lobe is provided with several instead of one. In both *Madrepora* and *Montipora* there is a more or less abundant trabeculate cœnenchyma. In *Madrepora* the budding is centrifugal, *i. e.* new buds arise below the apical corallite. In *Montipora* the apex consists of undifferentiated cœnenchyma and new buds are added above those existing, *i. e.* centripetally. He compared the condition to determinate and indeterminate inflorescence. The mode of budding in *Anacropora* is the same as in the genus *Montipora*. Ridley therefore suggests the establishment of two subfamilies, Madreporinæ and Montiporinæ, with characters based on this distinction.

The terms "centrifugal" and "centripetal" do not appear to

express accurately the precise modes of budding to which they are applied, and it would probably have been better had Ridley employed the botanical terms "determinate" and "indeterminate" to express the distinction in the case of branching species. In foliate species of *Montipora* the budding is centrifugal not centripetal, seeing that new corallites are added at the periphery. In branched specimens of *Madrepora* the buds arise around and are indirectly connected with an elongate corallite forming the axis of each branch and extending from its point of origin to the apex, where it always projects more or less. This corallite, often spoken of as the parent corallite, is usually of larger diameter than the others and often exhibits a better-developed series of septa. It is usually termed the apical corallite ("Endkelche," by the Germans), but axial corallite seems much more appropriate; the part of it which is "apical" and recognizable in surface view is only an insignificant part of its whole length. For similar reasons I propose to replace the term "lateral" corallite by "radial" corallite, excepting in the rare instances when these are arranged in lateral series on a flattened branch.

Although the types of budding indicated by Ridley form an essential distinction between *Madrepora* and *Montipora*, the type characteristic of *Madrepora* is confined to branches formed by the living colony during its growth: in other situations the buds are formed in a similar manner to those of *Montipora*. In specimens which form incrustations,—and all are incrusting in the first instance—new corallites are added peripherally from an undifferentiated mass of tissue which projects beyond existing corallites. It is only when certain of the corallites increase in length and thickness, so as to indicate the first formation of branches, by the development of buds around them, that the form of budding characteristic of *Madrepora* comes into operation. Frequently both types of budding take place at the same time in one colony; the one leads to branch formation, the other to marginal or basal extension. One not infrequently meets with specimens in which a colony of a younger generation forms an incrustation over the branches of a dead colony of the same species. In such cases new corallites are added form a marginal mass of undifferentiated tissue until the apex of the dead branch is reached, and only later, when independent growth begins, is the mode of budding changed. It also seems probable that the

immersed corallites which frequently occupy the lines of fusion between adjoining branches are formed by the primitive and not by the specialized mode of budding.

The classification of Actiniaria and Antipatharia is largely based on the structure of the polyps, and it seems extremely probable that before a natural classification of the Madreporaria is possible, much more information on this point must be available. In many cases difference of structure in the polyps is no doubt associated with a distinctive type of skeleton, but at present we are unable to use these characters to the best advantage. Still the marked bilateral arrangement of the septa in *Anacropora* and many *Montiporæ* appears to indicate an affinity with the genus *Madrepora* which, so far as we know at present, is not shared by any other genus. It therefore seems desirable to inquire whether Dana's views should be accepted as modified by Ridley, or whether we should regard *Madrepora* and *Montipora* as members of distinct, though closely allied, families.

Madrepora, with its axial corallites and radial bud-corallites, stands alone, and, so far as I am aware, there is no approach to this mode of colony formation in any other genus, taking into consideration the indirect means by which it is attained and the consequent absence of true cœnenchyma. It is also evident that both *Madrepora* and *Montipora*, as at present understood, will sooner or later be considerably subdivided, so that for purposes of convenience the course adopted by Ortmann has its advantages. The point, however, remains that the characteristic mode of colony formation in *Madrepora* is confined to the formation of independent branches and that at first in all colonies, and always so long as incrustation continues, the mode of budding is not characteristic. On this account it appears reasonable to suppose that the species of *Madrepora* form a specialized group which indicate their affinities in the incrusting stage. A final decision can only be arrived at when we know much more about the structure of the polyps and their relation to the skeleton which they produce; but in the meantime I prefer to adopt the course suggested by Ridley and divide the Madreporidæ into two subfamilies:—

Madreporinæ—gen. *Madrepora*.
Montiporinæ—gen. *Anacropora*.
gen. *Montipora*.